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# On Some Phyllocarids and the Origin of the Hoplocarida

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## INTRODUCTION

Recently I (1969b) described some new Middle Pennsylvanian hoplocarids. In addition to *Tyrannophontes theridion*, a rapacious species related to the stomatopod hoplocarids living today, two swimming, filter-feeding species were recognized, *Kallidecthes richardsoni* and *Aratidecthes johnsoni*. All these forms, though conforming to the basic hoplocarid body plan[1], exhibit such diversity as to indicate that the hoplocarids underwent an extensive radiation in the Late Paleozoic.

In discussing the evolution of the hoplocarids, I (1969a) suggested the possibility that the entire superorder Hoplocarida was independently derived from the leptostracans. Their origin would be separate and distinct from that of the caridoid eumalacostracans. At that time, reference was made (p. 281) to an "unnamed leptostracan" from the Middle Pennsylvanian Essex fauna of Illinois which seemed to fulfill many of the requirements of a hoplocarid ancestral type within the leptostracans. This paper will describe and discuss that animal.

In my 1969 papers the term "leptostracan" was used in the sense of Calman (1909), i.e., malacostracans were divided into two groups, Leptostraca and Eumalacostraca. Although this classification is

[1] These characters are: carapace covering the thorax; a kinesis dividing the cephalon into an anterior procephalon, which bears the eyes and first antennae, and a postcephalon; moveably articulated rostrum; thoracopods with a three-segment protopod, four segment inner branch, and a flap-like outer branch; enlarged abdomen; styloid telson with caudal furcae; and blade-like uropods.

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adequate for neozoological work, consideration of fossil forms requires some emendation of the taxonomy. Rolfe (1969) has set up a more useful systematics and his taxonomy will be used here. The term "Leptostraca" of my earlier papers is to be equated here with the subclass Phyllocarida as delineated by Rolfe.

In the following description references are made to specific specimens. Prefixes denote the collections in which they are to be found.

| | |
|---|---|
| PE | Field Museum of Natural History |
| A | Hunterian Museum, Glasgow, Scotland |
| HTP | Private collection of Mr. and Mrs. Ted Piecko, Chicago, Illinois |
| K | Private collection of Mr. and Mrs. James Konecny, Mokena, Illinois |

## SYSTEMATICS

### Subclass Phyllocarida Packard, 1879

### Order Hoplostraca, new

*Diagnosis.*—Carapace not hinged and covering no more than the thorax; abdomen considerably longer than the thorax; thoracopods not enclosed laterally by the carapace; anterior abdominal somites shorter than the posterior somites. (This order is principally based on the distinctive nature of the body tagma.) *L. Carb.—U. Carb.* (*M. Penn*).

### Family Sairocarididae, new

The characteristics of the family will remain, for the time being, the same as the characters of the order.

*Type.—Sairocaris,* Rolfe, 1963.

**Kellibrooksia,** new genus

*Diagnosis.*—Phyllocarid of moderate size; the carapace not covering the dorsal portion of the three posterior thoracomeres; the carapace laterally developed as large lappets which completely cover the sides of the thorax and only the bases of the thoracopods; most of the thoracopod not covered by the carapace; abdomen very elongate, somewhat over three times the length of the thorax; the first four abdominal somites relatively short, the last three somites long; pleopods on the first five abdominal segments; telson styliform with furcae as very short spines. *M. Penn.*

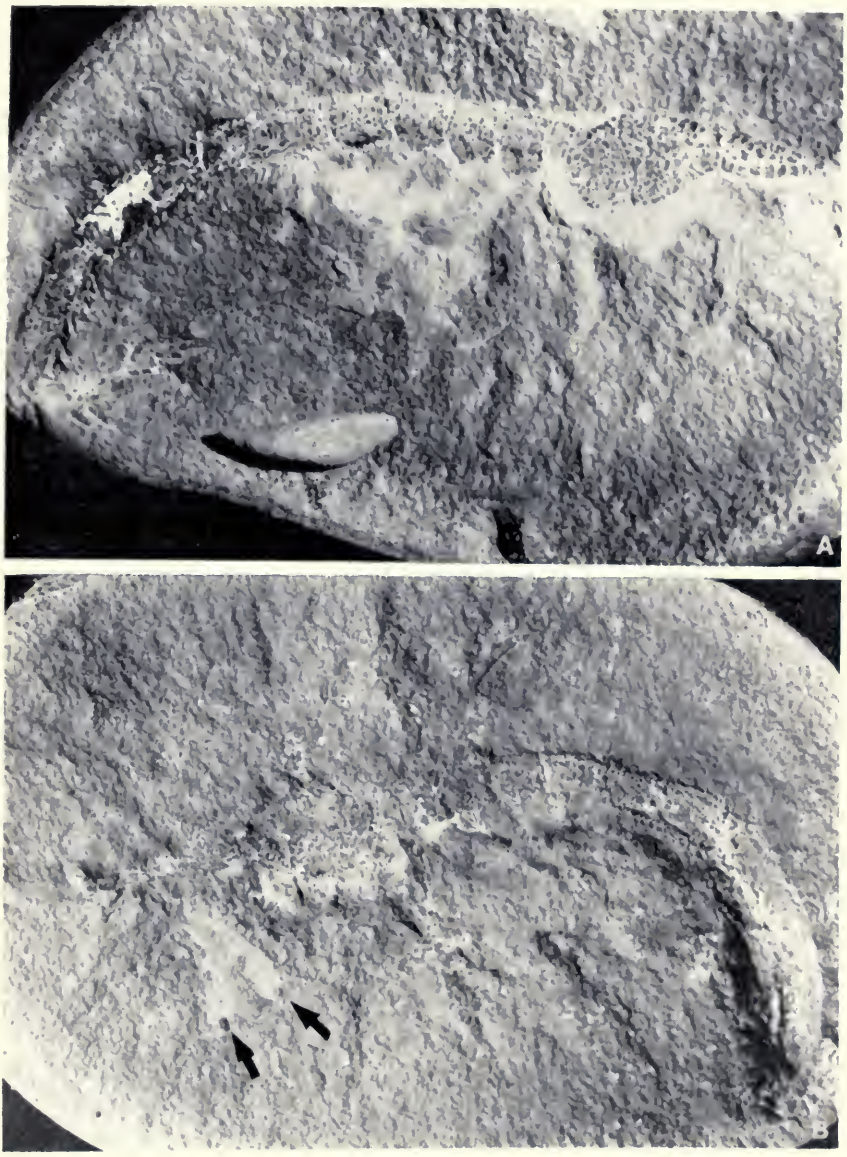


FIG. 1. *Kellibrooksia macrogaster*. A, HTP 86 displaying ghost-like appendage preservation and shape of carapace. × 2. B, HTP 4243 with "paddle-like" antennal scales. × 2.

FIG. 2. *Kellibrooksia macrogaster*. K 11-0009 with typical ghost-like appendage preservation and eye. × 2.

*Type of the genus.*—*Kellibrooksia macrogaster* Schram, new species.

*Remarks.*—This is a relatively rare crustacean of the Middle Pennsylvanian Essex fauna (Johnson and Richardson, 1966). Because of the resemblances of *Sairocaris elongata* (Peach) and *K. macrogaster* to the hoploid morphotype and their apparent distinctness from other phyllocarids, the Sairocarididae are made the basis of a separate order within the phyllocarids.

**Kellibrooksia macrogaster** new species. Figures 1–7.

*Occurrence.*—Francis Creek Shale, Carbondale Fm.

*Diagnosis.*—Since only one species is recognized at this time, the diagnosis of the species is the same as that of the genus.

*Description.*—This animal was approximately 5–6 cm. long from the anterior point of the carapace to the posterior tip of the telson. The carapace is very distinctive in outline, somewhat ax-like. Two definite regions of the carapace can be recognized: an anterior cephalic portion, ovoid in outline, covering the cephalic segments

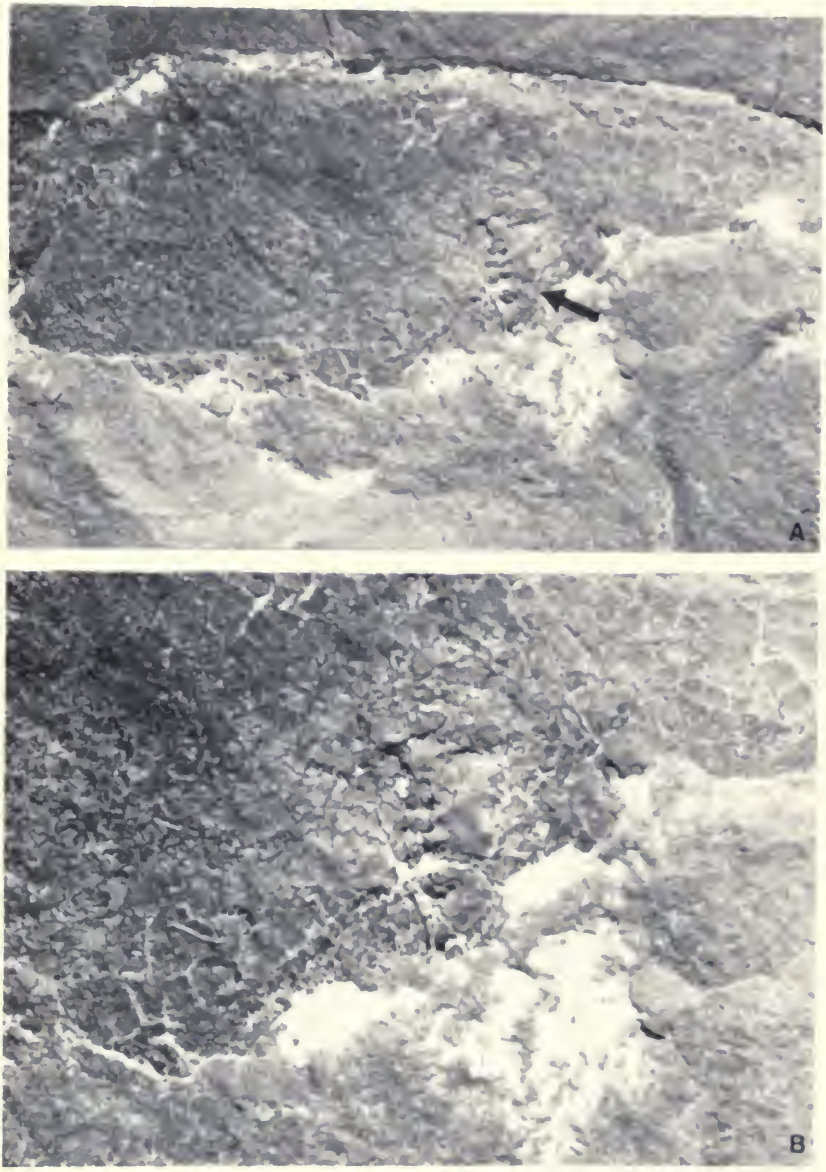


FIG. 3. *Kellibrooksia macrogaster*. K 11-0041. A, with carapace showing location of mandible. × 6. B, closeup of mandible.

anterior to the mouth, and a posterior thoracic portion developed as large "branchiostegal" lappets directed ventrad and posteriad (HTP 86, fig. 1).

Details of the cephalothoracic appendages are vague. All these appendages except the toothed mandibles were only slightly sclerotized. The first antennae were apparently directed forward. The second antennae seem to have had a large "paddle-like" scale (K 11-0009, fig. 2). K 11-0041 (fig. 3) displays a mandible with a heavy gnathal lobe located under the carapace between the anterior cephalic and posterior thoracic areas. The thoracic appendages have only been seen as ghost-like outlines and none of their structural detail is discernable (HTP 86); they are only basally enveloped by the carapace. Eye-like structures projecting from the anterior tip at the carapace have been observed on a number of specimens (K 11-0009, fig. 2; K 11-0017).

The carapace was free from at least the posterior thoracic somites. The thorax is nearly one-third the length of the abdomen.

The first four abdominal somites are short while the last three are at least twice as long as any one of these. The telson is long and styliform (PE 15647; K 11-0041, fig. 4), while the caudal furcae are developed as very small spines. Ghost-like pleopods can be seen on the first five abdominal segments of K 11-0045 (fig. 5) and other specimens, but again no structural detail can be discerned.

No sexual dimorphism was noted in the specimens at hand.

A reconstruction and a comparison with *Sairocaris elongata* are offered in Figure 6.

*Remarks.*—The inability to study the appendages of this animal in detail is disappointing, as much of the life style of crustaceans can be deduced from their appendages. In this regard, *Kellibrooksia* is like other fossil phyllocarids in which the appendages are typically not preserved. The ghost-like quality of the preservation might indicate a poorly sclerotized limb, perhaps foliaceous, probably adapted for swimming.

The relationship of the thoracic legs to the carapace in the sairocarids is surely very significant. John Cisne (personal communication) has investigated the feeding mechanism and behavior of *Epinebalia* in Tomales Bay, California. These animals feed on the detritus in the algal mats in which they live. They filter tremendous amounts of water in the course of a day, forming boli of detritus which they will then eat at their leisure. The carapace almost completely envelops the thoracic legs and helps to form a food groove. *Kelli-*

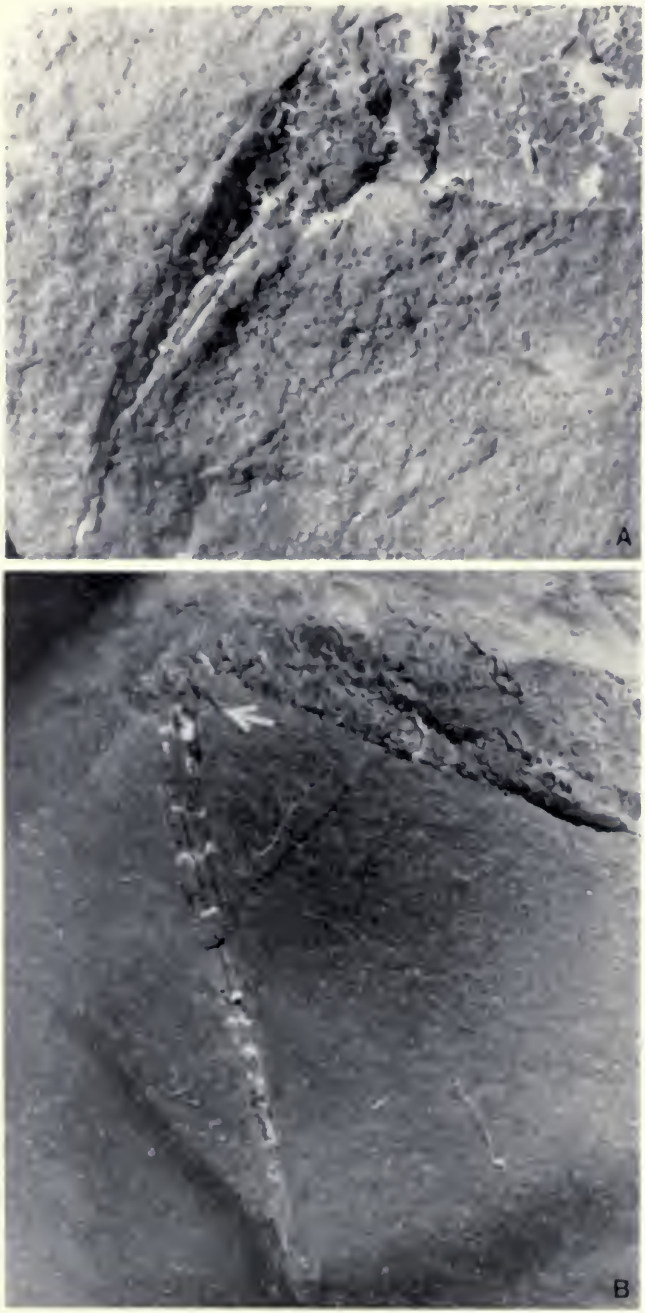


FIG. 4. Telson of *Kellibrookzia macrogaster*. A, PE 15647. × 7. B, K 11-0041 with arrow pointing to caudal furca. × 6.

*brooksia* does not employ the carapace in this manner. The thoracopods are laterally exposed and as a result *K. macrogaster* cannot have fed in the same manner as the living leptostracans, or even perhaps as the Archaeostraca, who also apparently enclosed the thoracopods with the carapace.

The overall body form is similar to that of a bottom dweller or animal with a burrowing habit. The shape is long and fusiform, and might indicate a behavior in which the creature at least partially buried itself at times. The mandibles are quite large with well-developed teeth; such usually indicate tearing or grinding. Although inconclusive, certain aspects of the anatomy of *K. macrogaster* are similar to those of modern stomatopod hoplocarids (such as body form, the elongate abdomen, the carapace not covering the posterior thoracomeres, and a considerable separation between the sense organs at the anterior tip of the cephalon and the mouth). Though this similarity may only be convergent, it does suggest affinities

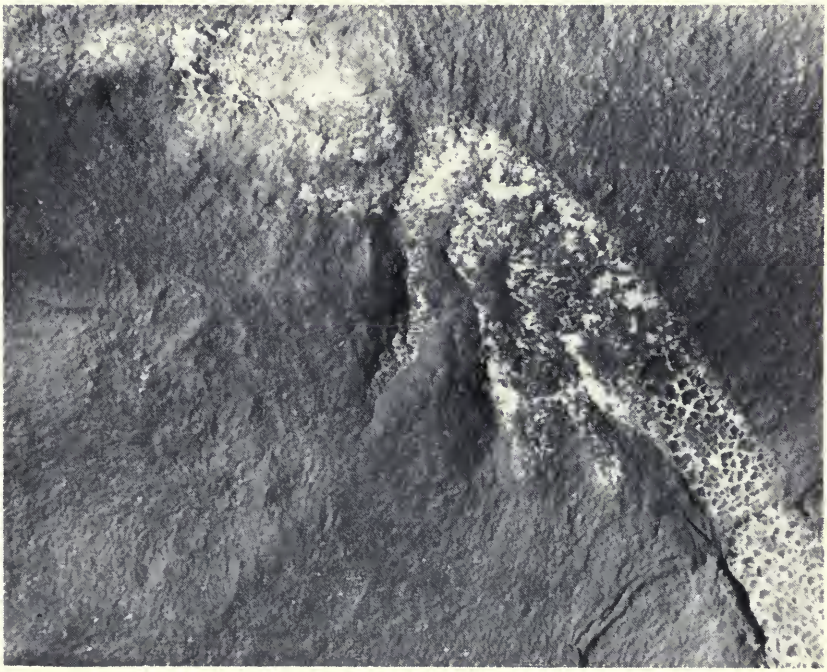

FIG. 5. *Kellibrooksia macrogaster*. K 11-0045, very poor preservation, but showing ghost-like pleopods. × 4.

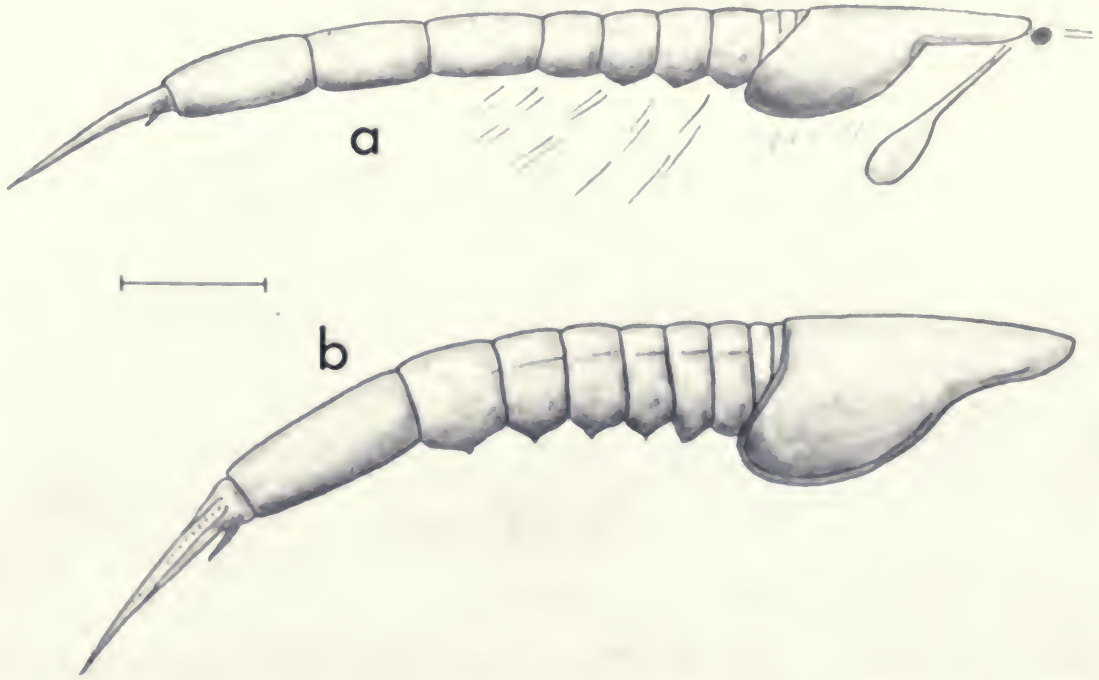


FIG. 6. Reconstructions. a, *Kellibrooksia macrogaster*, details on appendages remain sketchy because of the nature of the fossils. b, *Satrocaris elongata*, modified from Rolfe, 1969. Scale equals 1 cm.

between the two. No gut fillings have been noted in any specimens to date. Gut fillings commonly form prominent preservations in many of the crustacean species in the Essex fauna. The complete lack of these in *K. macrogaster* fossils might indicate a possibly carnivorous diet which did not contain a great deal of detritus.

One of the most peculiar aspects of the anatomy of *Kellibrooksia* is the large antennal (?) scales. Because of their position on the body, the scales appear to be associated with the second antennae. These structures are typically preserved in the position in which they are displayed in Figures 1 and 2. On a few specimens, however, such as PE 10363 (not illustrated), they are dropped back toward the thoracic portion of the carapace. The living leptostracans have no antennal scale, the exopod being absent on the second antenna, and the first antenna has a tiny scale associated with the first antennal flagellum.

There are several possible uses such a peculiar structure may have been put to: the condition of PE 10363 and the paddle-like nature of the structure suggests that the scale may have been lying along the side of the carapace or perhaps even inside the "branchiostegal" chamber. A twisting or oar-like movement could possibly have helped to set up a feeding current. The paddle portion of the scale could have helped to create a temporary suction-like pull either in the chamber or alongside the carapace, drawing a feeding current back toward or to the thoracic appendages. Although none of the living phyllocarids employ such a specialized structure to set up a feeding current, the much elongated cephalic area may have required it.

The scale might also have been directed laterad in life. A beating of the scales when the animal was on or near the muddy bottom could then have served to stir up the sediment. The animal might then have fed on the small animals and organic debris suspended in the cloud.

Another possibility lies in the scales being used as accessory swimming organs. In this case the paddles would have been extended outward like wings and used like oars in facilitating movement forward. One could also easily imagine copulatory, olfactory, fossorial, or defensive uses for these structures. Any of these suggestions could have been possible. There are no modern analogs with which to compare these scales since modern phyllocarids do not have a scaphocerite and no eumalacostracans have anything so big. As a


FIG. 7. Holotype of *Kellibrooksia macrogaster*, PE 12201. × 2.

personal preference, the first suggestion above seems acceptable. The nature of the jaws, however, may indicate that alternative two is more likely.

*K. macrogaster* is rare in the Essex fauna. Except for their appendages, the specimens are very nicely preserved, but they are too scarce for biometric analysis.

This genus is named in honor of my colleague Dr. H. K. Brooks of the University of Florida whose persistent efforts over the years have served to place the study of Paleozoic malacostracans on a sound scientific basis.

*Holotype.*—PE 12201 (fig. 7). Generously donated to Field Museum by Mr. and Mrs. Francis Wolff of Park Forest, Illinois.

## PHYLOGENETIC CONSIDERATIONS

Rolfe (1969) offers the most complete and recent discussion of phyllocarid evolution. Any presentation of primitive malacostracan phylogeny can be only tentative because of the incomplete nature of phyllocarid fossils. Phyllocarids were apparently among the earliest of arthropods. The middle Cambrian Burgess Shale fauna contains a number of carapaces referred to this group. But most of the fossil phyllocarid material of any age consists only of carapaces, carapace fragments, isolated telsons, and a few abdominal somites. Very seldom does one find an intact animal, and almost nothing is known of the appendages. Rolfe does offer a valuable summary of what little has been described on fossilized phyllocarid limbs.

Ideas on the evolution of the phyllocarids are consequently based on limited data. As Rolfe has indicated, one uses what is available for descriptive work, and this is frequently no more than one or two characters such as segment size or telson shape. We must still seek, however, within this poorly understood group, the ancestral eumalacostracan stocks even though only general body form can be consistently utilized.

In this regard, the Mazon Creek assemblages are of considerable assistance. Although important characters of the appendages are lacking in *Kellibrooksia macrogaster*, general form and relationship of parts are preserved, features typically unavailable in fossils from other localities. This is due to the intact-body and soft-part preservation of the Mazon Creek concretions.

From the Paleozoic hoplocarids an array of characters, the hoploid facies, was developed (Schram, 1969a, b) to elucidate a gen-

eralized morphotype. To what extent do the sairocarids fill the role of a phyllocarid ancestor to such an hoplocarid morphotype? The carapace does cover the thorax, although the dorsal portions of some of the posterior somites are exposed. The arrangement of the antennae seems to indicate a cephalic kinesis. The first antennae seem to be directed straight forward and the second antennae outward in some fashion, as in the Paleozoic hoplocarids. Even though the kinesis itself is not observable, such an arrangement has been interpreted as indicating a moveable area in the cephalon between the antennae. No rostrum has been seen on any hoplostracan specimens (it is possible that there may not have been any) and the exact nature of the appendages is unknown. But the abdomen is quite large, some three times the length of the thorax. In addition, it is the anteriormost abdominal segments of both *Sairocaris* and *Kellibrooksia* which are reduced. This reduction may prefigure the possible fusion of the first and second abdominal segments in the reduction to six abdominal segments in the stomatopod hoplocarids. The telson is styliform with furcae, although there are no uropods.

There appear to be some morphologic differences in *Sairocaris* related to age as indicated by size. I am led to this from study of the original descriptions of *Ceratiocaris elongata*, *C. scorpioides* (Peach, 1882), and *Acanthocaris attenuatus* (Peach, 1883) and examination of four specimens Dr. Rolfe loaned me from the Hunterian Museum. The abdomen to thorax ratios appear to be greater in the smaller, younger specimens. This ratio decreases in the larger, older specimens. Younger *Sairocaris elongata* seem to have relatively longer abdomens than the older adults.

The differences between *Kellibrooksia macrogaster* and *Sairocaris elongata* would seem to warrant maintaining separate genera for these forms. *Sairocaris* does not have the extreme development of the carapace into cephalic and thoracic regions. Although there is a slight delineation in *Sairocaris* of an anterior cephalic portion and a posterior thoracic area, the carapace as a whole is more sub-triangular than "ax-like." *Sairocaris* has only the two posterior thoracomeres exposed, and the enlarged abdomen does not quite reach the extreme of *Kellibrooksia*. The abdomen of *Sairocaris*, according to Rolfe, is only about 2½ times the length of the thorax, though Peach's (1882, 1883) original descriptions indicate an abdomen up to three to four times as long. That of *Kellibrooksia* is slightly over three times as long as the thorax. The proportions of the abdominal

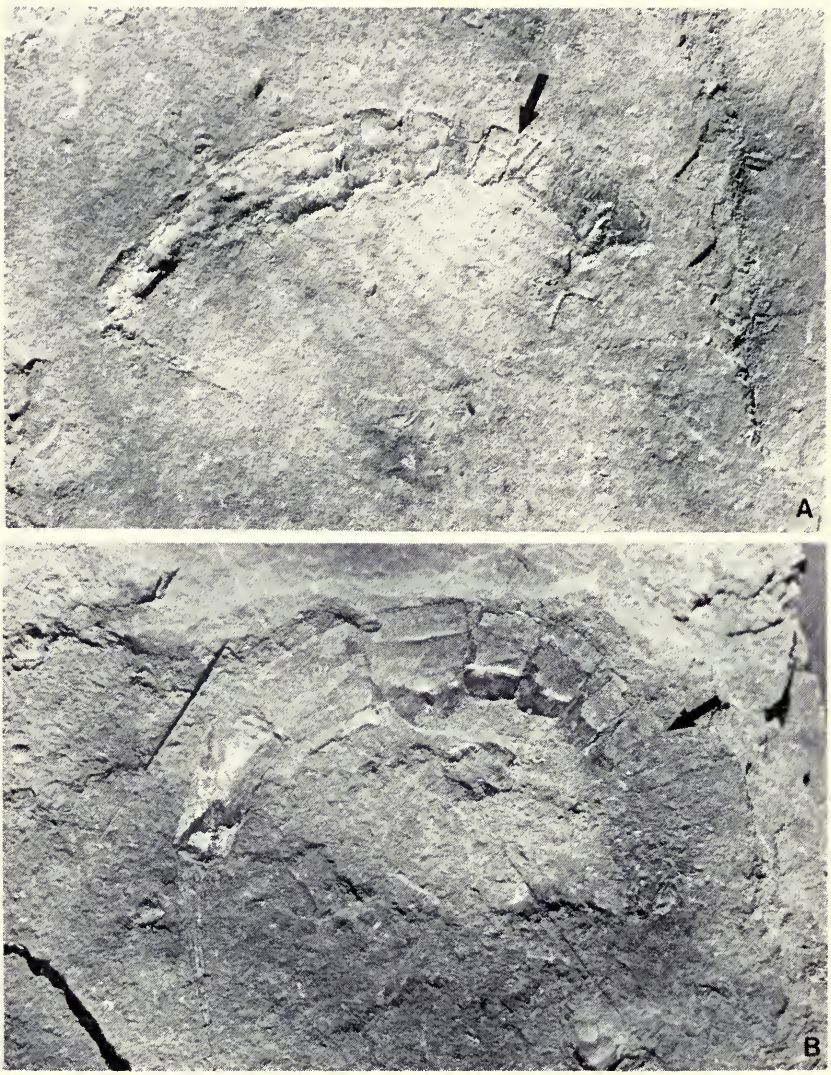


FIG. 8. *Sairocaris elongata*. **A**, A-2016b with posterior portion of thorax and abdomen of a younger individual. × 2. 3. **B**, A-2213 with thoracic fragment and abdomen of an older individual. × 2. 3. Arrows indicate thorax-abdomen boundary. Note the slightly longer abdomen in the apparently younger individual.

segments to each other are different. In *Kellibrooksia* the first four somites are all about the same size and reduced; the last three are all the same size and long. In *Sairocaris* the first six segments increase in size posteriorly while the seventh segment is greatly enlarged. Some examples of *S. elongata* from the Hunterian Museum are illustrated in Figure 8.

The differences noted here are certainly as great as or greater than those that separate other genera of phyllocarids. For example, the carapaces of the Devonian genera *Callizoe* and *Ptychocaris* are almost identical in outline. The anterior tubercle on *Callizoe* is more ventrally located than on *Ptychocaris*. *Ptychocaris* has some anterior nodes and a lateral ridge which *Callizoe* lacks. The differences between *Eleutherocaris* and *Montecaris* are small. *Eleutherocaris* has shallow anterodorsal grooves on its carapace instead of deep grooves, the lateral ridge is short and is only anterior and does not extend to the posteroventral spine. *Pygocaris* differs from *Aristozoe* in having a more pointed anterior horn, a pointed median posterodorsal process, and a thinner cuticle. In short, the differences between the above generic pairs (selected at random as examples) are ones of carapace decoration, differences which in eumalacostracans might be used to merely separate species. The differences between *Sairocaris* and *Kellibrooksia* are great enough to warrant a generic separation.

It would seem that the hoplostracans are certainly distinctive phyllocarids. Given the current knowledge and understanding of Paleozoic hoplocarids, this distinctiveness would seem to justify separating these two genera from the Archaeostraca and placing them in a separate order. The purpose of taxonomy is to reflect our current concepts of phylogeny (see fig. 9). It still appears that there is a distinct dichotomy within the Eumalacostraca. The hoploids exist, on one hand, with their emphasis on the abdomen as a receptacle for the major organs, and the caridoids, on the other, with their emphasis on the thorax as the visceral receptacle. Such a dichotomy must extend back into the phyllocarids. The hoplostracans could represent part of the line that culminated in the hoploids. Siewing (1956) interpreted the Lower Devonian *Nahecaris stuertzi* as a caridoid ancestral type; however, Rolfe (1969) disagrees with this. The lines leading through the phyllocarids to the hoploid and caridoid types should be recognized as our knowledge of phyllocarid fossils improves. Pre-hoploid and pre-caridoid phyllocarids probably

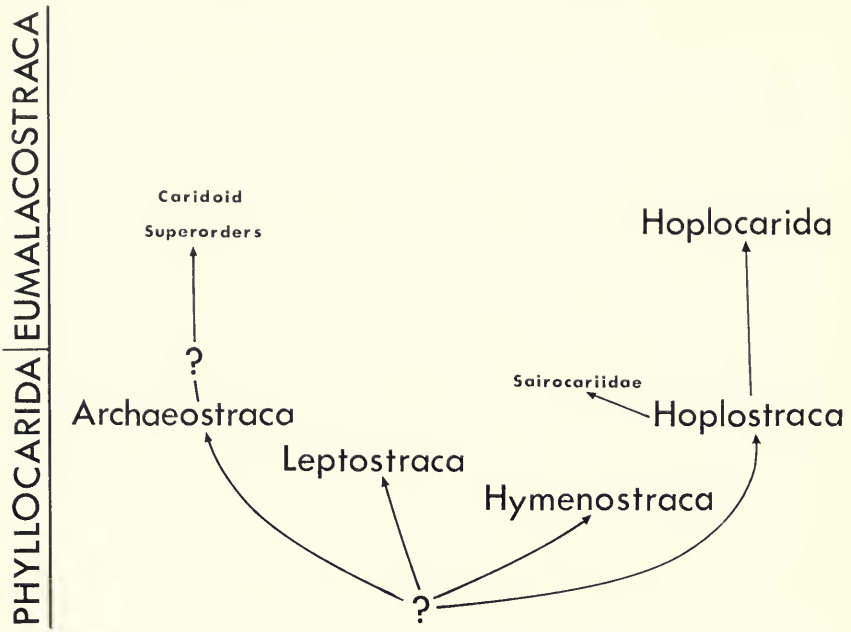


FIG. 9. Inter-relationships of the four orders of the subclass Phyllocarida and the various superorders of the Eumalacostraca. The order Hoplostraca, of which the sairocarids are members, probably contains the ancestral type of the Eumalacostracan superorder Hoplocarida. The Archaeostraca may be ancestral to the caridoid eumalacostracans. The Leptostraca (containing the only living forms of the Phyllocarida) seem to stand by themselves, but comparison with the fossil orders is difficult. The Hymenostraca, though sharing the unhinged carapace characteristic with the Hoplostraca, are also difficult to relate to other phyllocarids.

underwent extensive radiations in their own right as did other phyllocarid forms. There are late Paleozoic and Mesozoic-Cenozoic radiations of the eumalacostracans, and the phyllocarids without question had a similar history of their own in the early Paleozoic. We should be able to identify remnants of these radiations in the fossil record.

The sairocarids as now understood do not perfectly conform to our expectations of an ancestral type, being specialized in the form of the cephalothorax, the enlargement of the abdomen, and the peculiar nature of the antennal scales. The appendage anatomy could have been informative in this regard. The sairocarids thus probably represent a specialized part of the hoplostracan radiation. As *direct* ancestors of the hoploids they would tell us little. They do indicate, rather, the existence of an extensive and diverse early Paleozoic phyllocarid radiation.

## SUMMARY

A new species of Middle Pennsylvanian phyllocarid, *Kellibrooksia macrogaster*, from the Middle Pennsylvanian Mazon Creek Essex fauna of Illinois is described. The recognition of this form, combined with a related species from the British Lower Carboniferous, *Sairocaris elongata*, warrants the erection of a new order to accomodate the pre-hoploid phyllocarids.

## ACKNOWLEDGEMENTS

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